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A revision of the distribution of sea kraits (Reptilia, *Laticauda*) with an updated occurrence dataset for ecological and conservation research

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Abstract

The genus *Laticauda* (Reptilia: Elapidae), commonly known as sea kraits, comprises eight species of marine amphibious snakes distributed along the shores of the Western Pacific Ocean and the Eastern Indian Ocean. We review the information available on the geographic range of sea kraits and analyze their distribution patterns. Generally, we found that south and south-west of Japan, Philippines Archipelago, parts of Indonesia, and Vanuatu have the highest diversity of sea krait species. Further, we compiled the information available on sea kraits' occurrences from a variety of sources, including museum records, field surveys, and the scientific literature. The final database comprises 694 occurrence records, with *L. colubrina* having the highest number of records and *L. schistorhyncha* the lowest. The occurrence records were georeferenced and compiled as a database for each sea krait species. This database can be freely used for future studies.

Keywords

Amphibious snakes, Elapidae, geodatabase, distribution, marine, open access, sea snakes

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Introduction

Sea kraits (genus *Laticauda*) are a group of amphibious, marine snakes from the family Elapidae (Heatwole et al. 2005; Pyron et al. 2011; Shine et al. 2002, 2003), distributed in tropical and subtropical coastal waters of the eastern Indian Ocean, south-east Asia, and archipelagoes of the western Pacific Ocean (Heatwole et al. 2005).

The taxonomic status of the group has been and continues to be subject to much debate. For instance, Vitt and Caldwell (2009) recently elevated Laticaudinae as a separate subfamily within elapids. In contrast, Kharin and Czeblukov (2013) elevated the subfamily Laticaudinae to familial level (Laticaudidae) and divided the genus *Laticauda* into two genera (*Laticauda* and *Pseudolaticauda*), based on morphological characters. However, this split is not widely accepted (e.g., Elfes et al. 2013) and the sea kraits are considered to belong to a single genus, *Laticauda*. Furthermore, in a phylogenetic analysis of the group, Pyron et al. (2011) did not recognize any subfamilies within elapids, as none of the previously described ones (Elapineae, Hydrophiinae and Laticaudinae) formed well-supported monophyletic groups.

In contrast with the taxonomic disputes, from an ecological perspective, this clade is divided into three major complexes (Heatwole et al. 2005), which broadly overlap in geographic range, but differ in their relative use of terrestrial versus marine environments. Species from the "*Laticauda colubrina* complex" (Yellow-banded sea kraits, composed of *L. colubrina*, *L. frontalis*, *L. guineai*, and *L. saintgironsi*) are more terrestrial; species from the "*L. semifasciata* complex" (Black-banded sea kraits, composed of *L. semifasciata* and *L. schistorhyncha*) are more aquatic; and species from the "*L. laticaudata* complex" (Blue-banded sea kraits, composed of *L. laticaudata* and *L. crockeri*) are considered intermediate (Greer 1997; Heatwole 1999, Brischoux et al. 2013).

As amphibious animals, sea kraits have unique characteristics that allow them to perform well in both marine and terrestrial environments. For instance, as sea snakes, they display a paddle-shaped tail that allows them to move efficiently in the water (Brischoux et al. 2010; Brischoux and Shine 2011), but have retained terrestrial characteristics such as large ventral scales that allow them to crawl efficiently on land (Bonnet et al. 2005; Shine and Shetty 2001). Although they prey mostly on eels in coral reefs, sea kraits need to return on land (to digest, rest, slough their skin, mate, and lay eggs; Heatwole 1999) where they manifest a high degree of philopatry (Brischoux et al. 2009; Brischoux et al. 2007; Shetty and Shine 2002).

Interestingly, it has been recently shown that acquisition of fresh water is crucial for sea kraits (Kidera et al. 2013; Lillywhite et al. 2008) and that a combination of availability of fresh water on land and low oceanic salinity at sea may determine environmental tolerances and geographic distributions of sea kraits (Brischoux et al. 2012, 2013). Also, studies indicate that sea snakes may act as indicators of the effects of climate change (Lillywhite et al. 2008, 2014; Lillywhite and Tu 2011), and there is growing interest in their conservation (Bonnet 2012; Bonnet et al. 2009; Brischoux et al. 2009; Elfes et al. 2013).

As such, detailed knowledge regarding the distribution of sea kraits is key for applying conservation measures, planning conservation reserves, and evaluating the impact of human activities (Elith et al. 2006; Ferrier and Watson 1997; Funk and Richardson 2002; Rushton et al. 2004). In the present study, we review the information available on the geographic range of the three sea krait groups and analyze their distribution patterns. In addition, we provide an occurrence database for each sea krait species for use in future studies.

Materials and methods

Occurrence records

A database of sea krait occurrences was created using a combination of data extracted from online repositories (GBIF, HerpNet, iOBIS), from published scientific literature, and from field surveys. Most of the occurrences came from the marine environment, as data on terrestrial localities are scarce for this group. Because of philopatry, sea kraits generally avoid venturing very far from the shore line (Lane and Shine 2011a). Occurrences without spatial data were manually georeferenced to the finest scale possible using the information provided by the source and Google Earth 7. Country taxa lists or locations that could not be georeferenced due to lack of detailed locality descriptions (e.g., name of islands or provinces within countries; McCarty 1986; David and Ineich 1999) had to be excluded from our dataset, as the descriptions were too general. The resolution of the final dataset is 9 km and was projected to WGS84. This resolution is standardized in accordance with existing environmental data (e.g., Bio-ORACLE, www.oracle.ugent.be/) that can be used to answer various biogeographic, conservation or evolutionary questions.

Distribution patterns of sea kraits

Distribution maps for all species of sea kraits were created in ArcGIS 10.2 (ESRI 2011) by intersecting the occurrence points with the 100 km Military Grid System (MGRS) available on-line from the National Geospatial-Intelligence Agency (NGA 2014).

The Extent of Occurrence (EOO) and the Area of Occupancy (AOO) were calculated according to the methodology proposed by IUCN (2012) using ArcGIS 10.2 (ESRI 2011). The calculations for EOO were based on the occurrence records gathered, while the AOO also relied on the 100 km MGRS. In our study, the AOO is overestimated because of the 100 km MGRS used for measurements.

An optimized hot spot analysis was performed using the occurrence points for all species of sea kraits and the whole grid in order to identify statistically significant clusters of high values (hot spots) or low values (cold spots) (ESRI 2011). Subsequently, the

analysis was re-run using all occurrence points for the whole *Laticauda* group, but the area was limited to those cells that contained at least one occurrence. The aim was to detect areas in the distribution range of sea kraits that can be viewed as hot spots for the group (i.e., areas with high clustering of species).

Finally, the Shannon-Wiener diversity index was calculated for the group based on the number of occurrences in each cell of the grid, using the Marine Geospatial Ecology Tools (MGET) toolbox (Roberts et al. 2010). The classification scheme used for the index was based on the Natural Breaks (Jenks) algorithm (ESRI 2014).

Results

The final database was comprised of 694 unique records of occurrence at a spatial resolution of 9 km (Suppl. material 1). The bulk of these records belonged to the yellow-banded sea krait (*L. colubrina*, 64.55% of all records compiled), while the lowest number of occurrences was for *L. schistorhynchus* (0.86% of all records) (Table 1).

The EOO registered very high values for *L. colubrina* as a result of its wide distribution range, while *L. schistorhynchus* had the smallest EOO, with only 180.99km^2 (Table 2). The AOO was also the smallest for *L. schistorhynchus*, while the largest AOOs were for *L. colubrina* and *L. laticaudata* (Table 3).

The optimized hot spot analysis based on the whole MGRS grid identified the bulk of the range (western shores of Myanmar and Thailand, Indonesia, Malaysia, Philippines, Papua New Guinea, Solomon Islands, Vanuatu, and Fiji) as an area of high spatial clustering, with 99% confidence ($\bar{z}$ = 9.015; $\bar{p}$ = <0.001), while areas based on 95% confidence ($\bar{z}$ = 3.21; $\bar{p}$ = 0.001) generally omitted them (Figure 1). Important regions of high spatial clustering, but with a reduced degree of confidence (90%) ($\bar{z}$ = 2.84; p = 0.004), were located around the island of Palau and to the north of Papua New Guinea (Figure 1).

The Shannon–Wiener diversity index registered values between 0 and 1.089 and the diversity map created (Figure 2) showed high diversity values (>0.82) for sea kraits on the islands south-west of Japan and south-east of Taiwan, in the Visayan Sea from the Philippines Archipelago, in the northern part of Celebes Sea, on the northern shores of Halmahera, Indonesia, in New Caledonia around the atoll Ouvéa, and in the Coral Sea around the island of Efate, Republic of Vanuatu (Figure 2).

Discussion

Through the current study we provide the first set of comprehensive distribution maps for all exant species of sea kraits *Laticauda* spp. (but see also The IUCN Red List online maps). Following the pertinent suggestions of Heatwole and Cogger (2013), cases of vagrancy were excluded from the current analysis. Complementary analyses regarding

Table 1. Number of occurrence records available for each species in the *Laticauda* group.

Species	Number of occurrence records	% of total no. of occurrences
L. colubrina	448	64.55
L. frontalis	18	2.6
L. guineai	10	1.44
L. laticaudata	108	15.56
L. saintgironsi	75	10.81
L. schistorhynchus	6	0.86
L. semifasciata	29	4.18

Table 2. Extent of Occurrence (EOO) for the species of *Laticauda* group.

Species	Extent of occurrence (sq. km.)	Of which	
		% Land	% Ocean
L. colubrina	31,651,270.32	18.43	81.57
L. frontalis	93,874.79	7.99	92.01
L. guineai	6,461.75	83.27	16.73
L. laticaudata	27,350,493.24	15.74	84.26
L. saintgironsi	87,825.41	24.19	75.81
L. schistorhynchus	180.99	83.68	16.32
L. semifasciata	6,006,752.15	15.50	84.50

Table 3. Area of Occupancy (AOO) for the species of *Laticauda* group, calculated based on a 100 km Military Grid (NGA 2014).

Species	Area of occupancy (sq. km.)	Of which	
		% Land	% Ocean
L. colubrina	1,988,055.71	22.64	77.36
L. frontalis	63,909.17	9.03	90.97
L. guineai	13,228.66	69.00	31.00
L. laticauda	603,380.15	19.75	80.25
L. saintgironsi	152,370.06	13.67	86.33
L. schistorhynchus	11,239.95	2.30	97.70
L. semifasciata	204,637.92	14.29	85.71

the conservation and distribution of marine elapid snakes (including sea kraits) have been published by Elfes et al. (2013).

Laticauda colubrina has the largest range of any sea krait species (Table 1; Figure 3; Suppl. material 1), spanning from Tonga, in the south-east, through Fiji, Vanuatu, the Solomon Islands, New Guinea, Palau, most of the Indonesian coast, the Philipines, Taiwan, and reaching its northernmost limits in southern Japan and its westernmost limits in the Bay of Bengal, in the Andaman Islands and on the Myanmar coast (Figure 3; Suppl. material 1). Although the species exhibits a great degree of morphologi-

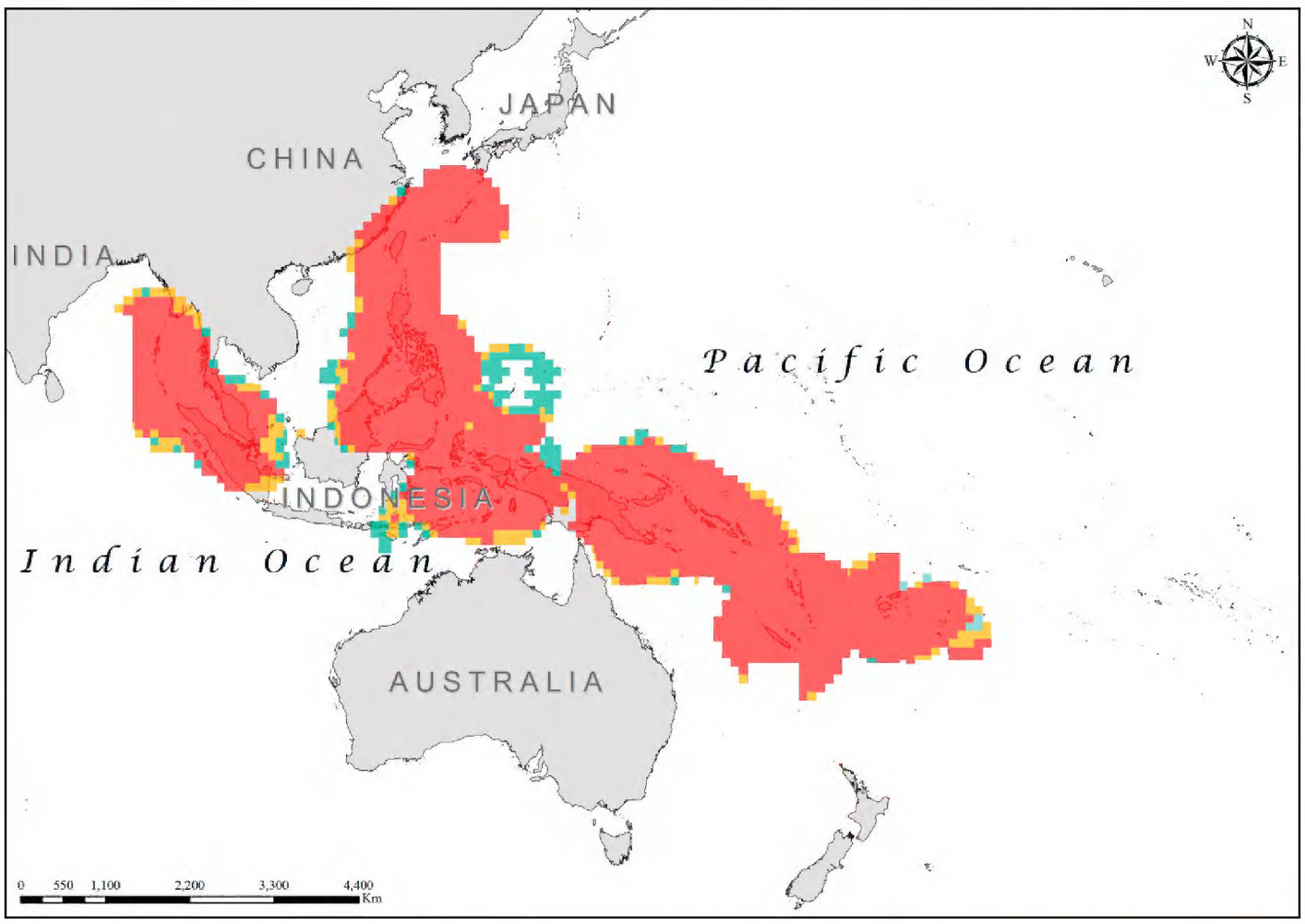

Figure 1. Distribution of hot spots for the *Laticauda* group (color codes reflect statistical confidence; red for 99% confidence level, orange for 95% confidence level, and green for 90% confidence level).

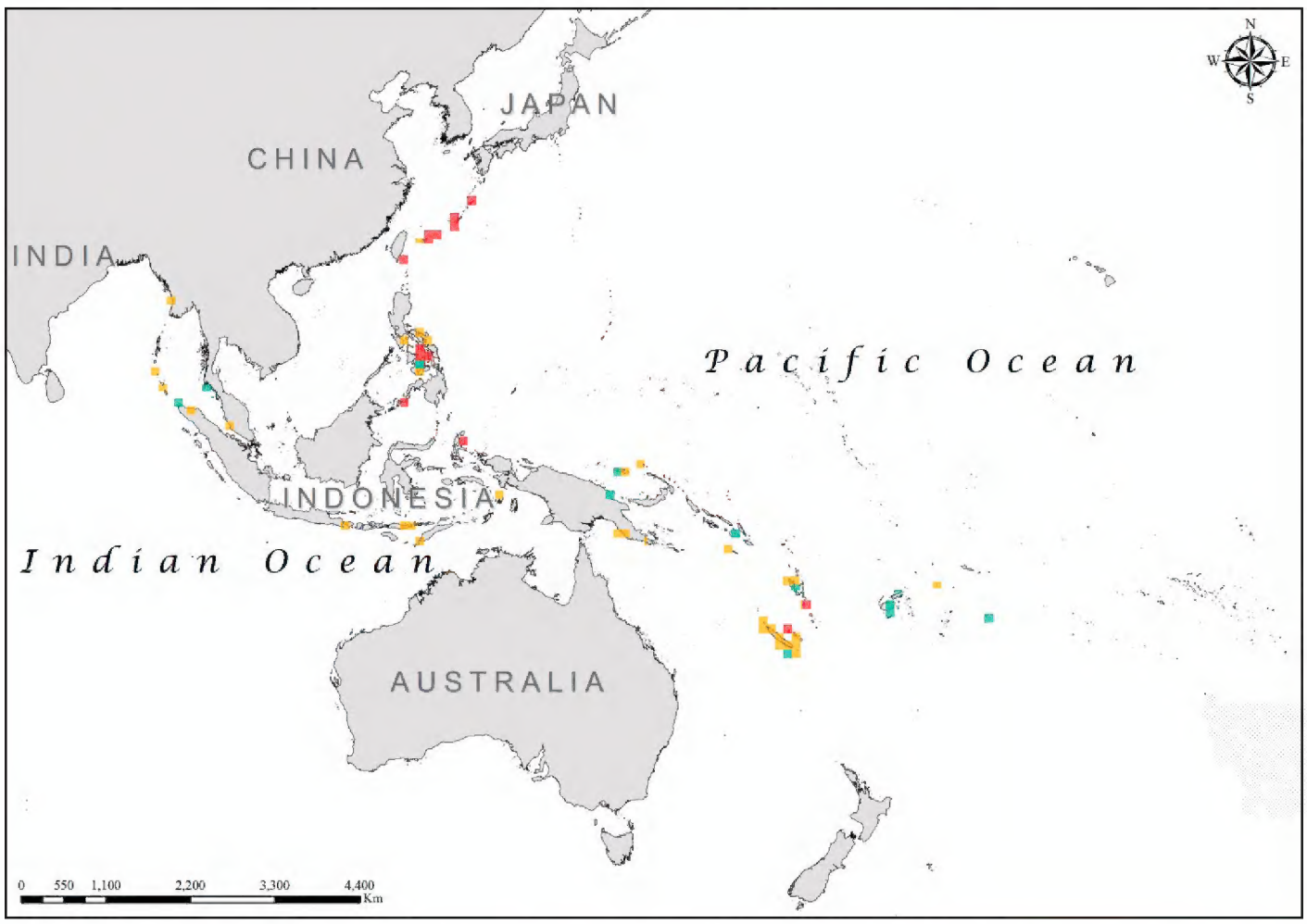

Figure 2. Shannon-Wiener diversity index for the *Laticauda* group (green: H' = 0.000001–0.56; orange: H' = 0.57–0.82; red: H' = 0.82–1.08).

cal variability across its distribution range, all populations are currently regarded as a single species (Heatwole 2010; Heatwole et al. 2005; Heatwole and Cogger 2013; Lane and Shine 2011b). In contrast, all other species of the *L. colubrina* group have very narrow distribution ranges. *Laticauda frontalis* is considered endemic to Loyalty Islands and the islands of Vanuatu (Cogger and Heatwole 2006) (Figure 4; Suppl. material 1). Except for this latter location, the available records indicate that the species is sympatric with *L. colubrina* throughout Vanuatu (Figures 3 and 4; Suppl. material 1). *Laticauda guineai* has a very small distribution range, known from only two areas in southern Papua New Guinea (Heatwole et al. 2005) (Figure 5; Suppl. material 1). *Laticauda saintgironsi* is endemic to New Caledonia, including the Loyalty Islands (Figure 6; Suppl. material 1), as reported by other authors (Cogger and Heatwole 2006; Heatwole and Cogger 2013). In the Loyalty Islands, the species occurs in sympatry with *L. frontalis* (Figures 4 and 6; Suppl. material 1).

Laticauda laticaudata has a very wide range, similar to that of *L. colubrina* (Figures 3 and 7; Suppl. material 1), but the range of *L. laticaudata* is much more fragmented and the species' EOO and AOO are considerably smaller (Tables 2–3) than those of *L. colubrina.* The easternmost location of *L. laticaudata* is the Island of Niue while the northernmost and westernmost limits for the species are the same as for *L. colubrina* (Figures 3 and 7; Suppl. material 1). However, *L. laticaudata* also occurs in New Caledonia, where it is sympatric with *L. saintgironsi*, and in Vanuatu, where it is sympatric with *L. frontalis* (Figures 4, 6, and 7; Suppl. material 1). Contrasting with this very broad range, the only other sea krait species from the *L. laticaudata* group, *L. crockeri*, is known from a single location, the Lake Te'Nggano from Rennell Island, Solomon Islands (e.g., Elfes et al. 2013; Heatwole and Cogger 2013). The ecology of this species is virtually unknown (but see Cogger et al. 1987) and the species is considered highly vulnerable (Elfes et al. 2013), thus ecological and conservation research should be prioritized for this species.

The *L. semifasciata* group comprises another two species with contrasting and allopatric distribution ranges: *L. schistorhyncha*, endemic to the Island of Niue (Figure 8; Suppl. material 1) (Heatwole and Cogger 2013), and *L. semifasciata*, with a relatively wide but fragmented distribution range, southern Japan being its northernmost limit. Although the southern limit for the species was previously considered to be the Maluku Islands (Heatwole and Cogger 2013), our database indicates an extension of the known range, with new records from southern Indonesia (Figure 9; Suppl. material 1).

With the exception of one species, all sea kraits presented a terrestrial EOO < 25%. The notable exception is *L. guineai* for which more than 80% of the EOO comprises terrestrial surfaces. In a recent attempt to assess the conservation status of the world's marine elapids, Elfes et al. (2013) have also calculated values for the extent of occurrence of several *Laticauda* species. The EOO calculated by us for *L. frontalis* (93,874 km^2) considerably exceeds the value reported by Elfes et al. (2013), which was less than 15,000 km^2. This discrepancy is due to a coarser grid (NGA 2014) that was used in our study.

For the entire Hydrophiinae, the greatest diversity of hot spots comprise the Gulf of Thailand, the Java Sea, the Timor Sea, Arafura Sea, and the Gulf of Carpentaria

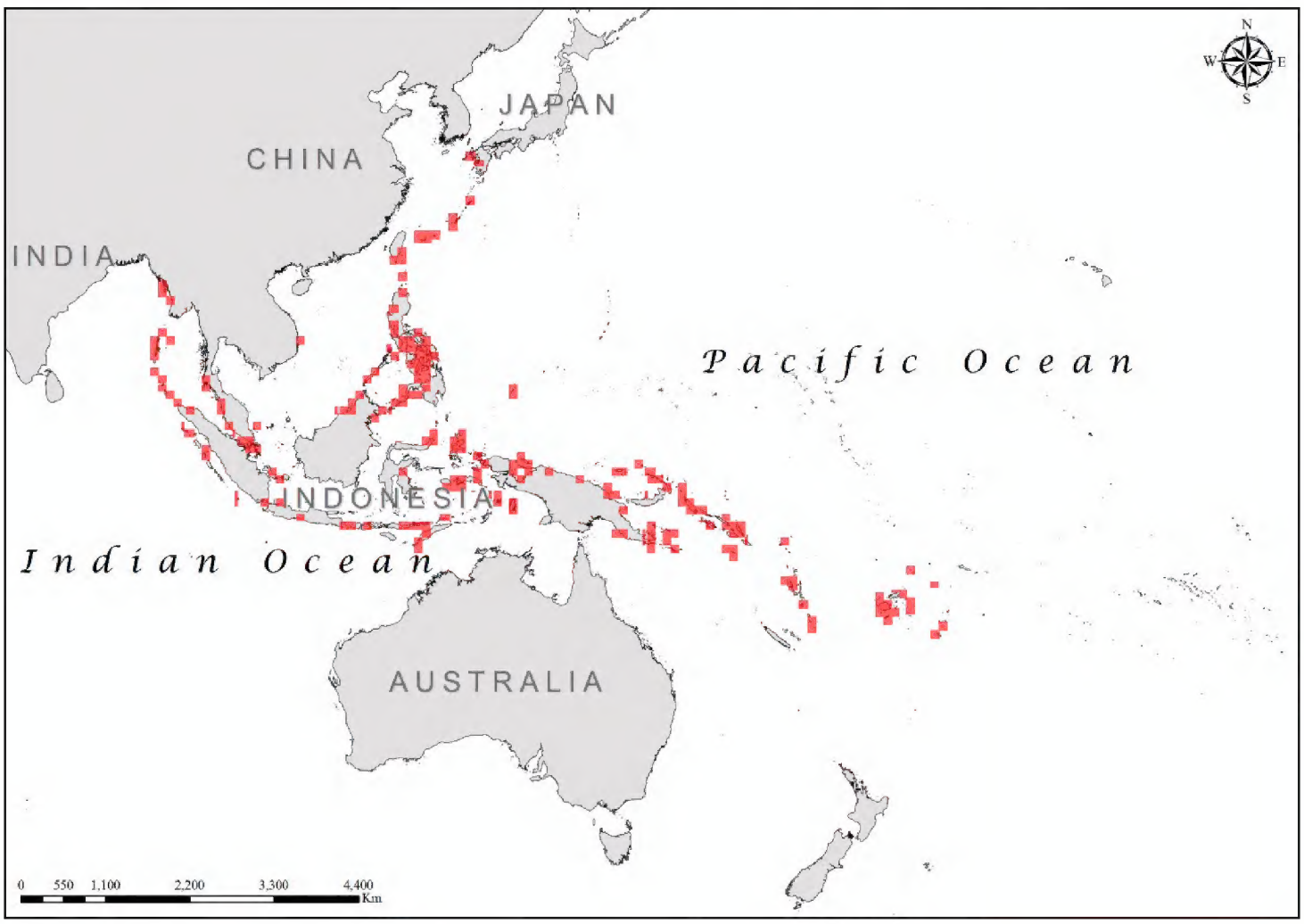

Figure 3. Distribution of *L. colubrina*.

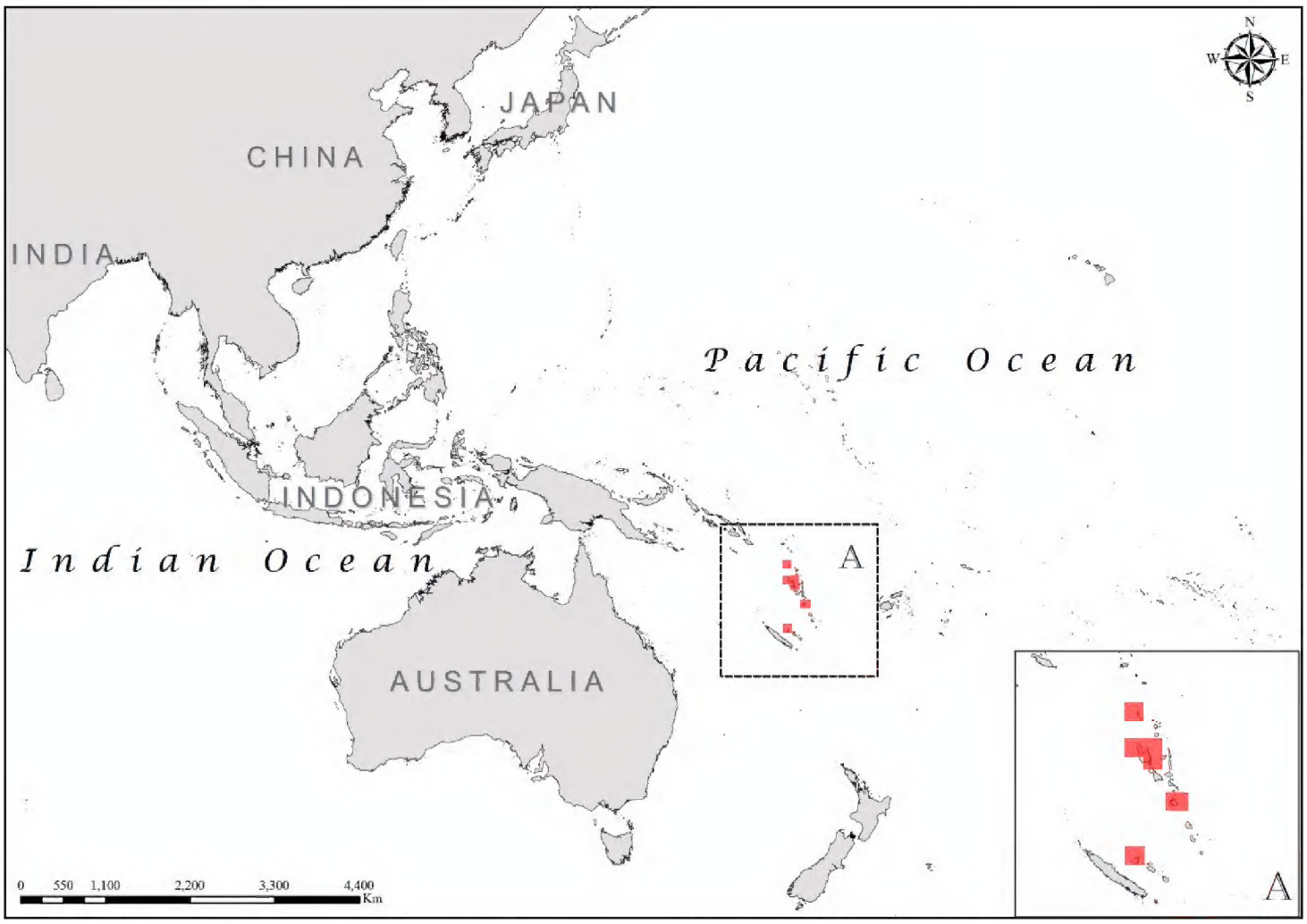

Figure 4. Distribution of *L. frontalis*, regional view and zoomed in (**A**).

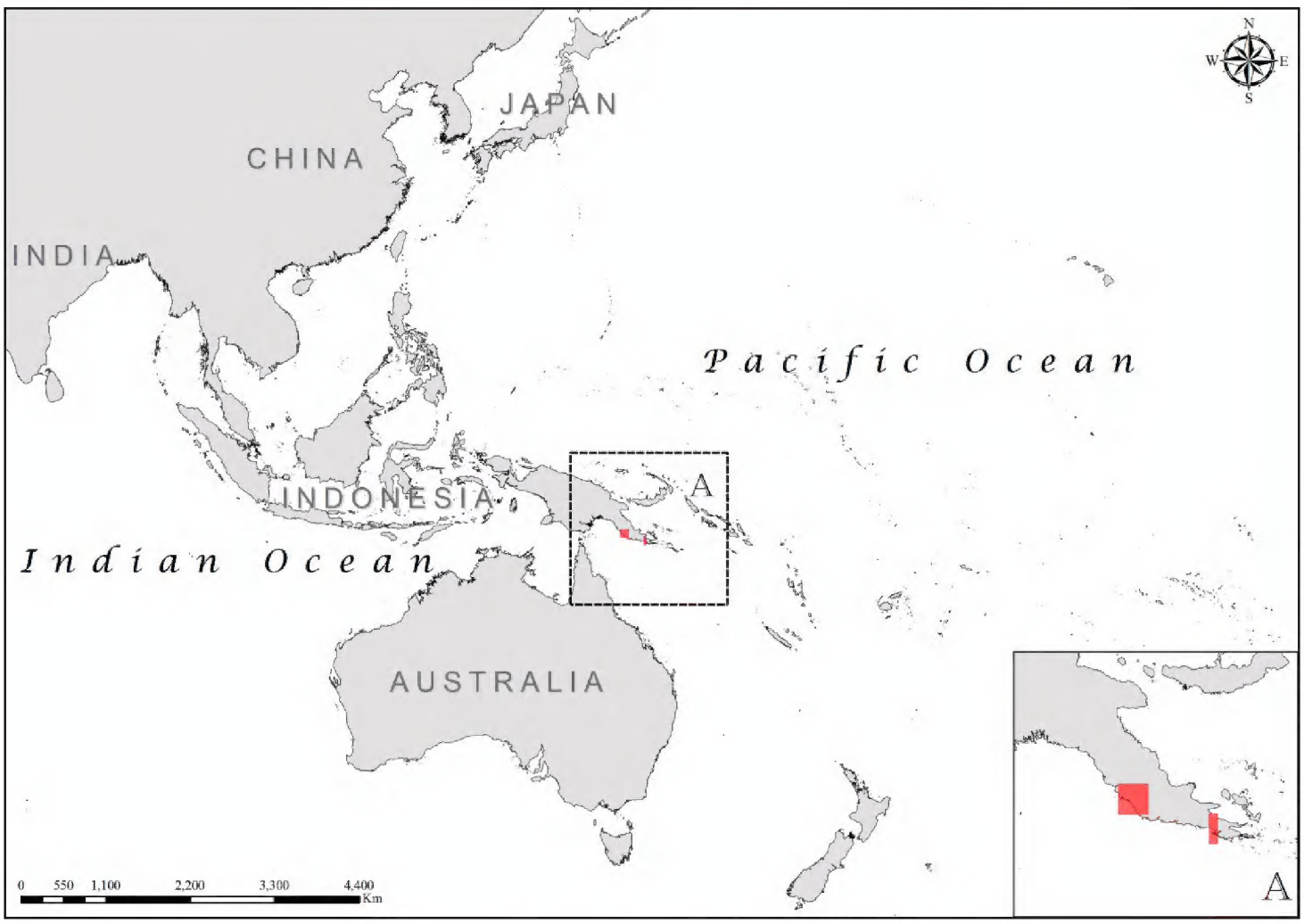

Figure 5. Distribution of *L. guineai*, regional view and zoomed in (**A**).

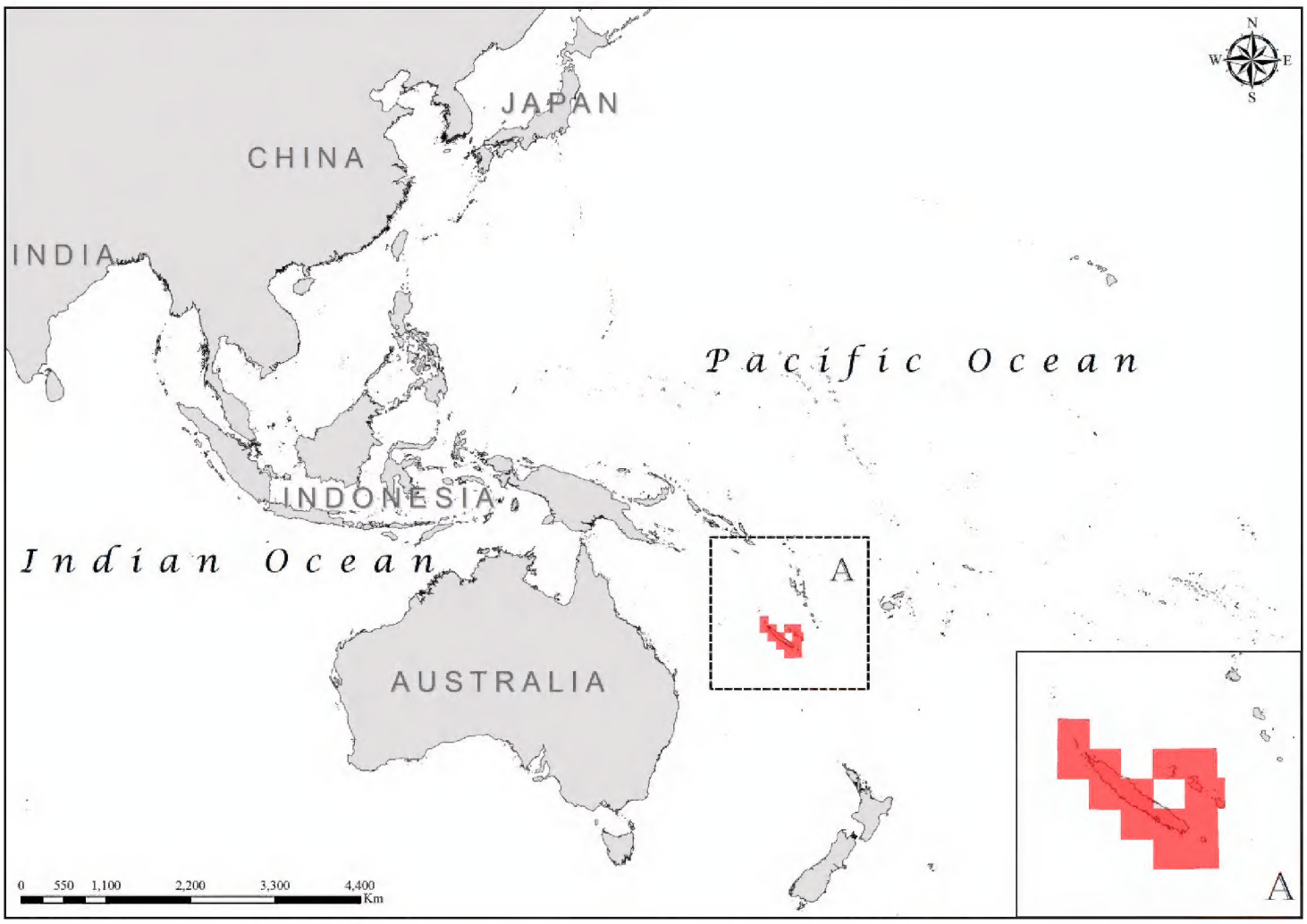

Figure 6. Distribution of *L. saintgironsi*, regional view and zoomed in (**A**).

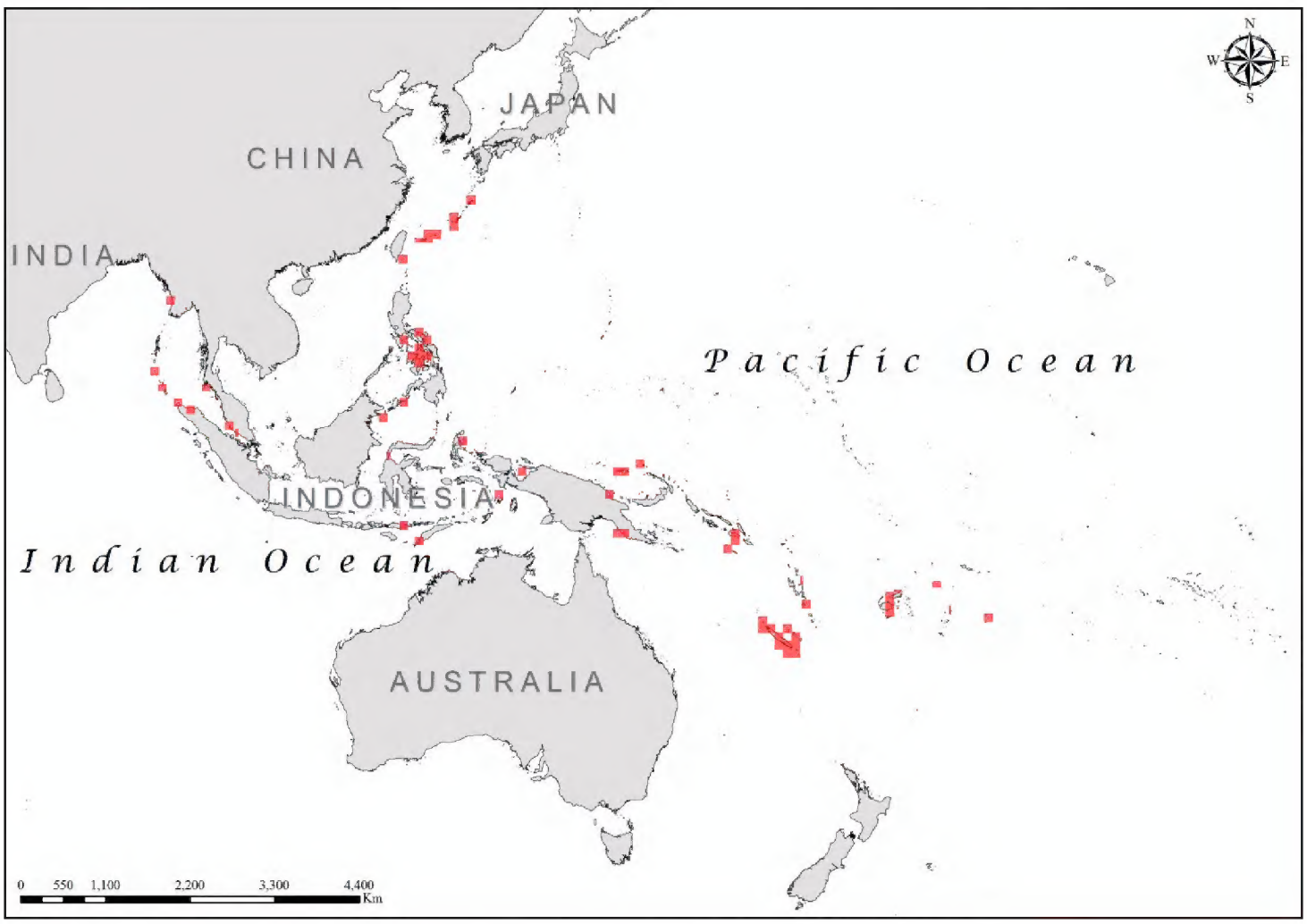

Figure 7. Distribution of *L. laticaudata*.

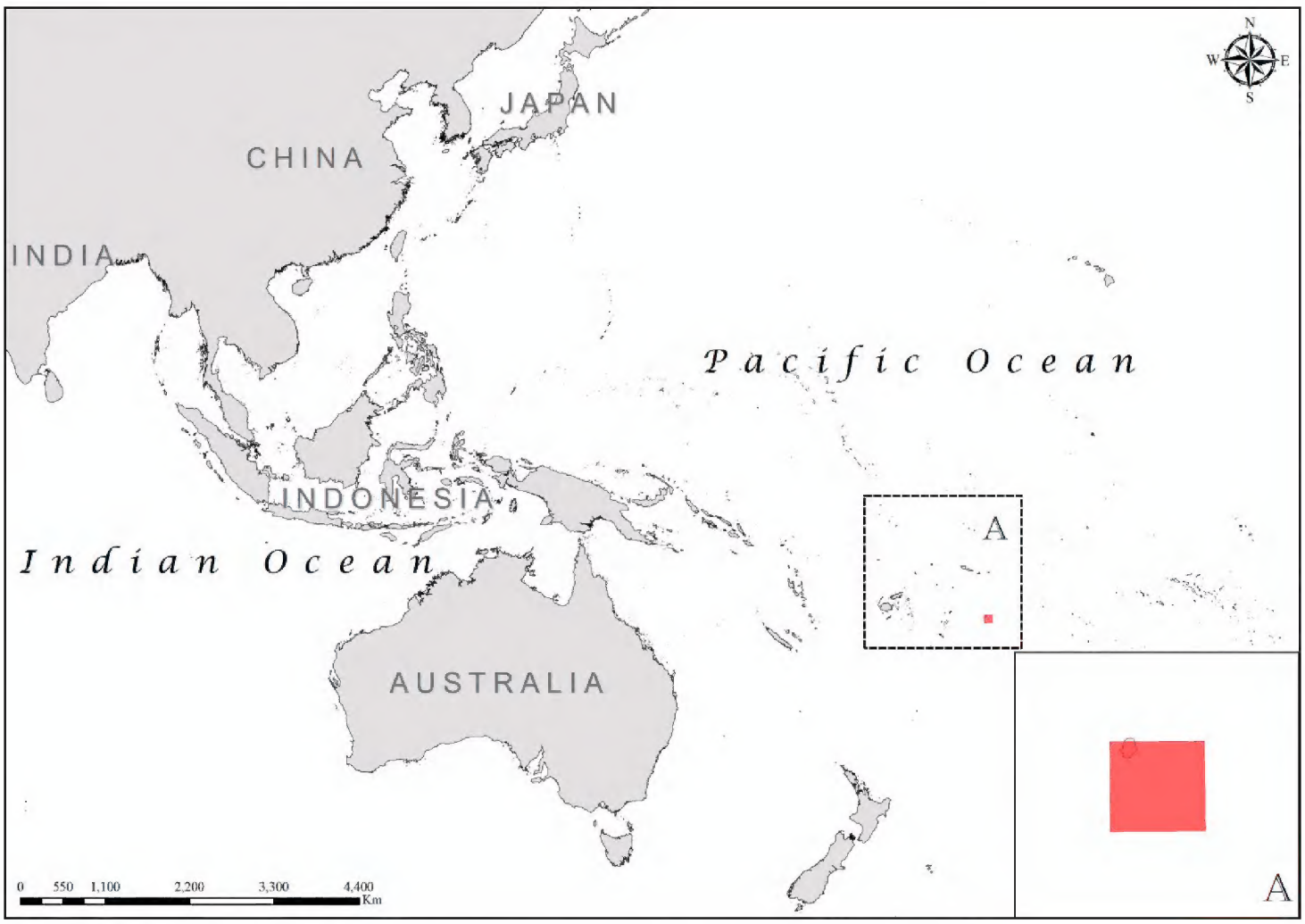

Figure 8. Distribution of *L. schistorhynchus*, regional view and zoomed in (**A**).

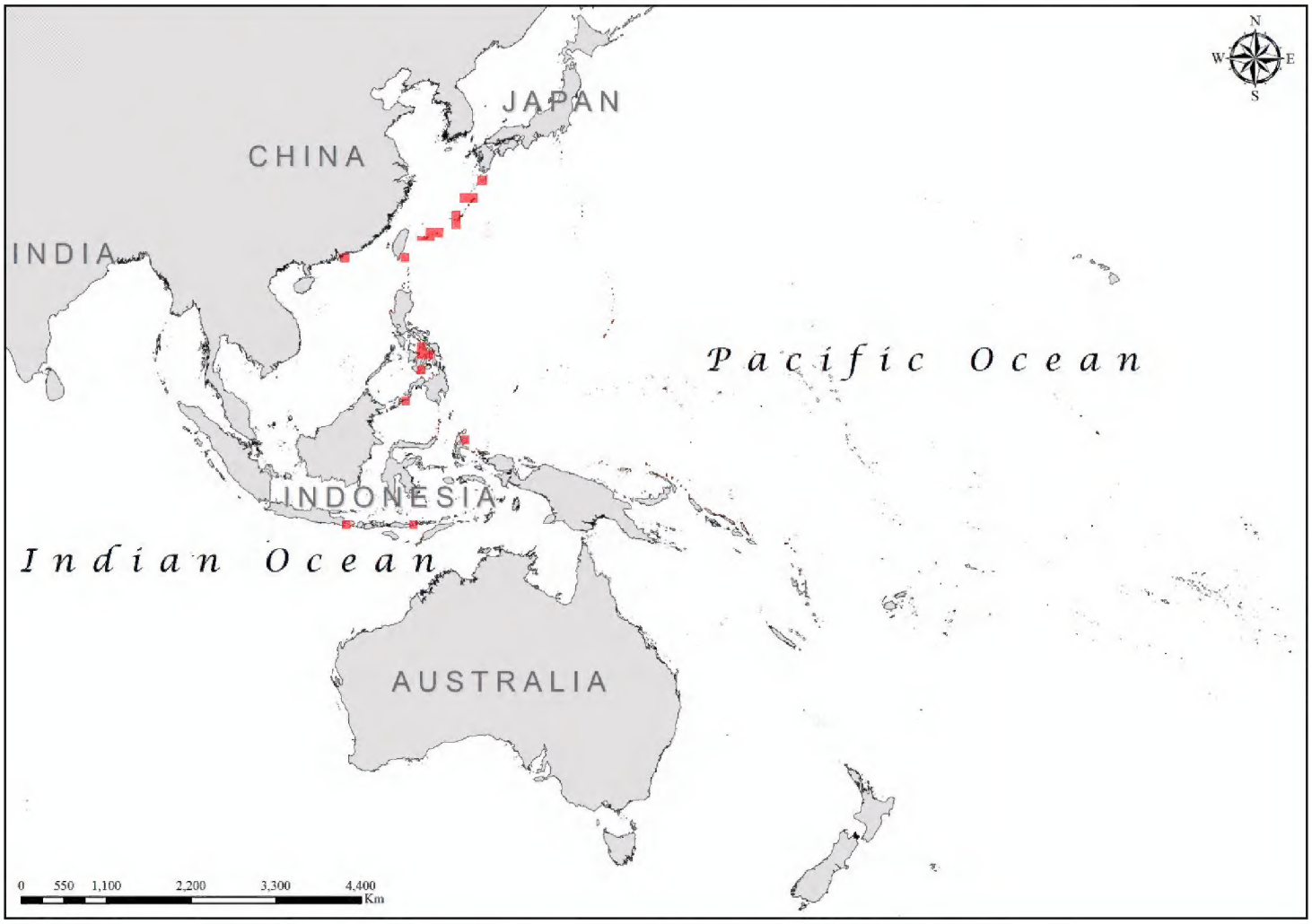

Figure 9. Distribution of *L. semifasciata*.

(Elfes et al. 2013). Remarkably, the areas of greatest diversity of sea kraits specifically, as identified by the current study, are outside the major hot spots for Hydrophiinae (Elfes et al. 2013), despite broad preferences of most marine Elapids for benthic habitats and coral reefs (Heatwole 1999). This difference suggest that the center of origin for the transition to marine life in Hydrophiinae and in sea kraits may be different, albeit geographically relatively close (Brischoux et al. 2012).

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Supplementary material 1

Occurrence dataset of all sea krait species included in this study

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Data type: Occurrences

Explanation note: Geodatabase of occurrence records of all sea krait species compiled in the current study.

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